A NEW AUSTROMEGABALANUS (CIRREPEDIA, BALANIDAE) FROM THE PLIOCENE OF NAMAQUALAND, CAPE PROVINCE, SOUTH AFRICA

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(With 3 figures and 1 table)

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ABSTRACT

A preliminary investigation of fossil barnacles from shallow marine coastal plain deposits exposed at Hondeklip, Namaqualand coast, South Africa, revealed the presence of a new species of austral megabalanine, *Austromegabalanus (Notomegabalanus) kensleyi* sp. nov., in an Upper Pliocene formation informally termed the 50-metre Package. This is the first extinct barnacle described from South Africa and, with the possibility of additional new species being recognized in future work, the biostratigraphic utility of barnacle assemblages for nearshore deposits of the South African margin is promising.

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INTRODUCTION

Shallow marine deposits, ranging in age from Early Pliocene to Late Pleistocene, underlie the terrestrial cover sands of the coastal plain along the Atlantic margin of South Africa. Mining of diamonds in these marine deposits adjacent to the Namaqualand coast creates temporary exposures that provide opportunities to examine the sedimentology and sample the fossil content. Hitherto the fossil molluscs have received attention, the most recent work being that of Kensley & Pether (1986), which presents a list of taxa and discusses the composition and biogeographic affinities of the fauna. This paper describes the first new species of barnacle recognized from the coastal plain marine deposits of South Africa. The specimens were obtained from the diamond mine at Hondeklip Bay (Fig. 1). The stratigraphy, sedimentary geometry, depositional environments, and evidence for the age of the deposits in this area are summarized in Pether (1986).

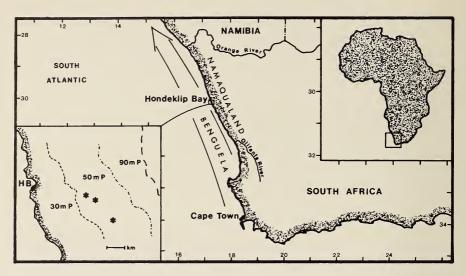


Fig. 1. Provenance of Austromegabalanus (Notomegabalanus) kensleyi sp. nov. Broken lines in left insert show inland (subsurface) limits (transgressive maxima) of main marine formations underlying the coastal plain. Informal formation labels record elevation of transgressive maximum, e.g. 50-metre Package. Asterisks indicate localities where the new species was obtained.

DESCRIPTION

Family **Balanidae** Leach, 1817 Subfamily Megabalaninae Newman, 1979 Genus *Austromegabalanus* Newman, 1979 Subgenus *Notomegabalanus* Newman, 1979

Austromegabalanus (Notomegabalanus) kensleyi sp. nov.

Figs 2-3

Diagnosis

Relatively small, smooth shell with single row of parietal pores and porous radii; no transverse septa in either. Thick scutum of high relief, no exterior radial sculpture; small, triangular, deeply excavated, lateral depressor pit, deep adductor muscle pit, no definite adductor ridge. Tergum not beaked and with short, broad spur at less than two-thirds its own width from basi-scutal angle; broad, very shallow spur furrow; no definite depressor crests.

Distribution

Upper Pliocene of the Namaqualand coastal plain, west coast of South Africa.

Material

Holotype. SAM-PQ-HB337a, one complete shell with opercula removed from cluster on boulder, Hondeklip Zone 12A (30°19′29″S 17°18′21″E).

Paratypes. SAM-PQ-HB337b-df, 110 complete shells from same cluster as holotype, many with opercula and bases. SAM-PQ-HB1261, cluster of approximately 30 shells on *Striostrea margaritacea* (Lamarck, 1819) valve, one of which contained an articulating opercular pair, Hondeklip Zone 4A.

Additional material. SAM-PQ-HB321, unattached cluster of 9 shells without opercula, Hondeklip Zone 12A. SAM-PQ-HB180, disarticulated shells and scuta, Hondeklip Zone 12A. SAM-PQ-AV984, 4 shells without opercula, Avontuur A, T2/3. SAM-PQ-AV1067, 3 shells without opercula, Avontuur A, T2/3.

Measurements

Holotype. Height 4,2 mm, carino-rostral diameter 11,1 mm, scutum occludent margin 3,7 mm, tergum scutal margin 2,6 mm.

Largest shell. SAM-PQ-AV984a, height 6,3 mm, diameter 14,7 mm. Largest scutum. SAM-PQ-HB180, occludent margin 6,2 mm.

Description

Shell relatively small (~1 cm basal diameter). Specimens from smooth, uncrowded substrate (Fig. 2C) are low-conical with regular and smooth exteriors, have pentagonal to pointed-ovate, moderately toothed orifices about one-third carino-rostral diameter, and thin, flat bases. Those from uneven and crowded substrata (Fig. 3C) are more globulo-conical with relatively larger orifices, rugose exteriors and have cup-shaped bases (up to 1 cm deep), often with irregularly cellular underlayers.

Parietes with single row of open longitudinal pores, ovoid in section near apex, subrectangular near basis; internally ribbed, ribs usually on lower portion but may extend almost to sheath, short secondary ribs sometimes on larger specimens; basal denticles conspicuous with correspondingly small tapered ridges on lower ribs; sheath about half the length of plate, lower margin usually separated from wall by moderate to very shallow concavity. Many specimens still have a rose-pink hue colouring the sheath. Darker radial lines on exteriors of parietes correspond to the underlying septa. Radii inset from parietes, transversely porous although upper pores may be infilled; sutural edges regularly and densely septate with denticles on lower edges of septa (Fig. 3D), articulating surfaces on adjacent parietes with corresponding low, upward denticulations. Alae thin and broad, crenate sutural edges sometimes visible. In unabraded specimens, such as the SAM-PQ-HB337, the radii summits are obliquely truncated and the alae have steeply oblique summits, usually projecting above the opposite sloping radii. In more abraded specimens the summits are approximately parallel to the base. Basis radially porous, with shallow furrows corresponding to the underlying pores.

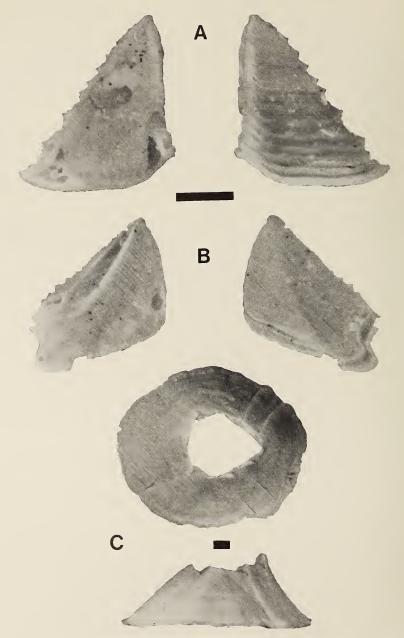


Fig. 2. Holotype of *Austromegabalanus (Notomegabalanus) kensleyi* sp. nov., SAM-PQ-HB337a. A. Interior and exterior views of scutum. B. Interior and exterior views of tergum. C. Apertural and lateral views of shell. Scales = 1 mm.

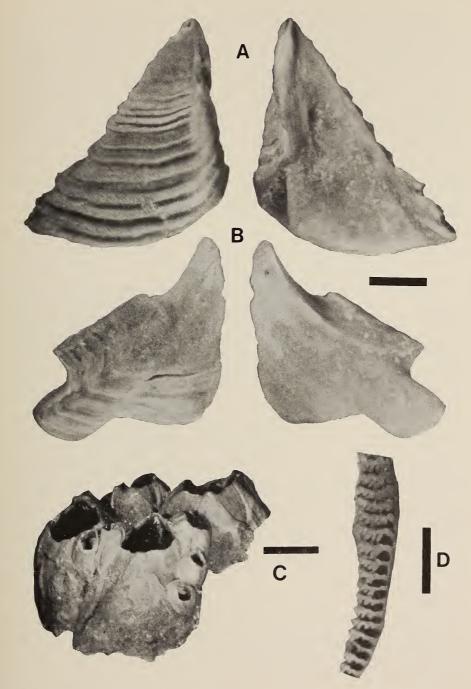


Fig. 3. Austromegabalanus (Notomegabalanus) kensleyi sp. nov. A-B. Large paired scutum and tergum from paratypes, SAM-PQ-HB1261. Scale = 1 mm. C. Shell cluster from same paratypes, set on *Striostrea margaritacea* valve. Scale = 5 mm. D. Sutural edge of radius showing austral megabalanine denticulation. Scale = 1 mm.

Scutum thick, of high relief; concave exterior with prominent growth ridges, every alternate one denticulating occludent margin; no radial sculpture; basal margin convex and about two-thirds length of occludent margin; tergal margin about three-quarters length of occludent margin and on exterior raised as a low ridge from apex to basi-tergal angle before being strongly but quite narrowly reflexed, the ridge enhancing the concavity of the exterior; a shallow groove is often present along the reflexed tergal segment. Articular ridge high, about four-fifths of tergal margin in length and reflexed over relatively narrow articular furrow; articular ridge thins basally, ending in a closely rounded-off corner above concave terminal edge; outer face shallowly concave and faint grooves are generally visible. Adductor muscle scar large, ovate and conspicuously deep, usually being visible without magnification, even in small scuta. No obvious adductor ridge but a low, rounded swelling is usually present beside adductor tergal margin and laps on to the basal flank of articular ridge. Lateral depressor pit small, narrowly triangular and deeply excavated, usually with slightly overhanging sides. Occludent margin interiorly reflexed, producing marginal ridge that basally overhangs rostral depressor insertion.

Tergum carinal and basal margins convex, scutal margin straight; exterior with low growth ridges, more pronounced on scutal portion; no radial sculpture. Spur furrow broad, open and very shallow to flush; margins slightly incised. Exterior carinal portion gently convex, exterior scutal portion usually slightly outwardly deflected. Articular margin quite narrowly reflexed at approximately right angle, rugose, forming ridge along scutal margin of articular furrow; articular furrow broad, moderately deep; articular ridge relatively thin, moderately high and partially overhanging furrow near apex. Apex not beaked, area of transverse ridges small; interior of valve below apex with several irregular grooves; carinal depressor crests effectively absent but faint grooving sometimes visible. Spur short and wide, approximately as long as broad; occupying from quarter to third of basal margin, situated about half to two-thirds own width from basi-scutal angle; basal margin segments slope towards spur, basi-scutal margin concave. Scutal end of spur closely rounded off, carinal corner very widely rounded off and almost a continuous curve from basal margin to scutal end. On interior of valve spur is only little raised and has a flat to slightly concave inner face. On the largest tergum available (Fig. 3B) the spur is seen to be relatively more developed than is the case in smaller specimens and the upper scutal margin is eroded.

Etymology

The species is named for Dr Brian Kensley of the Smithsonian Institution, Washington, D.C., in recognition of his contributions to the knowledge of the southern African fossil molluscan fauna.

DISCUSSION

The porous radii establish the Namaqualand specimens as belonging to a megabalanine genus. The classification system followed here is that of Newman (1979), with the modifications proposed by Buckeridge (1983). In the former work, Balanidae with porous radii were allocated to a new subfamily Megabalaninae. Taxa possessing radii with secondary denticles on the lower sides of primary denticles only were recognized as pan-austral Southern Hemisphere endemics and assigned to two new genera, Austromegabalanus and Notomegabalanus. The former genus is distinguished by beaked terga and closed spur furrows, the latter by non-beaked terga and open furrows. However, Buckeridge (1983), in his monograph on the fossil barnacles of Australia and New Zealand, expressed the opinion that the differences in tergal morphology, with respect to spur furrow and beak, between Austromegabalanus and Notomegabalanus are not sufficiently strong to justify full generic separation. He thus proposed that *Notomegabalanus* be regarded as a subgenus of Austromegabalanus. Furthermore, the taxa with porous outer parietal laminae were removed from Notomegabalanus and placed in a new genus Fosterella. With secondary denticles on the lower sides of the primary radii denticles only, this species from Namaqualand is confirmed as an austral megabalanine. The open spur furrow and lack of a strongly beaked tergum place it in the subgenus Notomegabalanus.

Listed in Table 1 are the fossil and extant species of *Notomegabalanus*, together with their approximate geological ages. *Austromegabalanus* s.s. and *Fosterella* have been included to provide a complete list of these related austral genera.

The austral megabalanines have not always been confined to the Southern Hemisphere. Fossil occurrences of *Notomegabalanus* in Tertiary deposits on both the Pacific and Atlantic coasts of North America have been recorded by Zullo & Guruswami-Naidu (1982) and Zullo (1986). As discussed by Newman & Foster (1987), this distribution suggests that *Notomegabalanus* has had a Tethyan and an amphitropical history, the present austral endemism being due to Northern Hemisphere extinction and Neogene dispersal via the West Wind Drift. *Notomegabalanus* is considered more generalized than *Austromegabalanus* s.s., whilst *Megabalanus* s.s. is the most highly evolved of the megabalanines (Newman 1979). The presence of an undescribed species of *Notomegabalanus* in the Oligocene of Oregon (Zullo 1986) is consistent with such a relationship. The Neogene radiation of these related taxa and the extinctions due to Pleistocene glaciations (which particularly affected *Fosterella* and *Notomegabalanus*), are evident in Table 1.

Austromegabalanus (Notomegabalanus) kensleyi is rendered distinct from all other species of the subgenus by its short, broad, rounded tergal spur at less than its own width from the basi-scutal angle, especially if this character is considered simultaneously with the very shallow spur furrow and subdued expression of the spur ridge on the valve interior.

The comparison of A. (N.) kensleyi with the austral species of Notomegabalanus indicates that the deep, narrowly triangular lateral depressor pit distinguishes

TABLE 1

Fossil and extant species of *Austromegabalanus* and *Fosterella*. Geographical location: N = Northern Hemisphere occurrence; S = Southern Hemisphere occurrence; WNA = Western North America; ENA = Eastern North America; IN = India; NZ = New Zealand; AUS = Australia; SAF = South Africa; SAM = South America; ANT = Antarctica; SOI = Southern Ocean Island.

Species	N/S Loc.	oc.	Oligocene	Miocene	Pliocene	Pleistocene Recent	Recent
Austromegabalanus (Austromegabalanus) victoriensis Buckeridge, 1983		AUS		1			
Austromegabalanus (Austromegabalanus) nigrescens (Lamarck, 1818)	S	NS					
Austromegabalanus (Austromegabalanus) piscoensis Carriol et al., 1987		AM					
Austromegabalanus (Austromegabalanus) psittacus (Molina, 1782)		AM					
Austromegabalanus (Austromegabalanus) cylindricus (Gmelin, 1780)		AF				1	
Austromegabalanus (Austromegabalanus) isolde (Holthuis & Sivertsen, 1967)	S	ō					
Austromegabalanus (Austromegabalanus) zulloi Newman, 1979	S	ō					
Austromegabalanus (Notomegabalanus) sp. Zullo, 1986		NA VNA					
Austromegabalanus (?Notomegabalanus) insperatus Zullo & Guruswami- Naidu. 1982	z	VNA					
Austromegabalanus (Notomegabalanus) wilsoni (Zullo, 1969)	z	VNA					
		NA NE					
Austromegabalanus (Notomegabalanus) lepidus Zullo, 1986	z	ANS					
Austromegabalanus (?Notomegabalanus) squillae (Daniel & Ghosh, 1963)		z					
	S	Z					
Austromegabalanus (Notomegabalanus) decorus argyllensis Buckeridge, 1983	S	ζZ					
Austromegabalanus (Notomegabalanus) decorus decorus (Darwin, 1854)		Z					
Austromegabalanus (Notomegabalanus) campbelli (Filhol, 1885)	S	Z					
Austromegabalanus (Notomegabalanus) kensleyi sp. nov.		AF					
Austromegabalanus (Notomegabalanus) algicola (Pilsbry, 1916)		AF				1	
Fosterella chathamensis Buckeridge, 1983		72		•		ı	
Fosterella tubulatus (Withers, 1924)		72				1	
Fosterella tubulatoides (Newman, 1979)		SAM				1	
Fosterella hennigi (Newman, 1979)	S	LZ					

the scutum of the new species from other representatives of the subgenus. The lack of a definite adductor ridge separates the new species from all other austral *Notomegebalanus* species except *A. (N.) algicola* (Pilsbry, 1916) which, however, has a very broad scutum. The absence of scutal radial sculpture is a feature in common with *A. (N.) algicola* and *A. (N.) campbelli* (Filhol, 1885). The basal end of the articular ridge of the new species is not pointed or dependant, as is the tendency in other austral species of *Notomegabalanus*. The lack of a tergal beak distinguishes the new species from the weakly beaked *Notomegabalanus* species of New Zealand.

The shells of A. (N.) kensleyi are slightly larger than those of A. (N.) algicola but smaller than the New Zealand representatives of the subgenus, the ribbed A. (N.) campbelli being closest in dimensions. Whereas the latter and A. (N.) decorus (Darwin, 1854) have transverse septa in the parietal pores, the new species does not, a feature in common with A. (N.) algicola and evidently A. (N.) miodecorus Buckeridge, 1983.

In the Northern Hemisphere, the extant *Balanus (Megabalanus) squillae* Daniel & Ghosh, 1963, possesses austral megabalanine radii. This rather cryptic and very small species from the coast of Madras is parasitic on a stomatopod, *Squilla* sp. It is problematic in possessing a tergum that is non-beaked but has a closed spur furrow. On the basis of the overall resemblance of the opercula to those of *A. (N.) algicola*, this species has been tentatively placed in *Notomegabalanus* by Henry & McLaughlin, 1986. The small broad scutum with an adductor ridge further distinguishes it from the new species. *Austromegabalanus (N.) wilsoni* (Zullo, 1969) from the Upper Pliocene of California also possesses an unbeaked tergum with a closed spur furrow and similarly has been placed in *Notomegabalanus* on the basis of its overall resemblance to *A. (N.) algicola*. Additional discoveries of such species that do not strictly conform to the definition of *Notomegabalanus* might render a redefinition of the subgenus or erection of another subgenus advisable.

The scutum of A. (N.) wilsoni resembles that of A. (N.) kensleyi in respect of the small, deep, lateral depressor pit and lack of an adductor ridge, but differs in respect of the straight basal margin, radially aligned pits on the exterior of some specimens and overall larger size. Austromegabalanus (N.) lepidus Zullo, 1986, from the Pliocene of the Western North Atlantic is a species of comparable size to that of A. (N.) kensleyi but the scutum, although also lacking an adductor ridge, is thin with a shallow lateral depressor pit and occasionally has exterior radial striae. In addition to the deep spur furrow, the tergum of A. (N.) lepidus differs from the new species in the strongly concave scutal margin, presence of distinct depressor crests, and radially striate exterior scutal portion. The opercula of A. (?N.) obliquus (Ross, 1964) (Pliocene, Western North Atlantic) have not been recovered but that species is larger than the new species and has externally ribbed parietes with deeply inset radii. The opercular valves of A. (?N.) insperatus Zullo & Guruswami-Naidu, 1982 (Late Miocene, California), are also unknown but the shell is also larger than A. (N.) kensleyi and has prominent external ribs.

It is noteworthy that of all the representatives of *Notomegabalanus*, the opercula of the new species are overall most similar to those of the extinct genus *Fosterella* Buckeridge, 1983. This applies particularly to the deep, small, scutal lateral depressor pit (this feature having been considered a defining character of *Fosterella*) and the short tergal spur and shallow spur furrow. In general appearance the opercula of *Fosterella tubulatoides* (Newman, 1979) from the Late Pleistocene of the continental shelf off Tierra del Fuego are closest. However, several other features remain to distinguish the opercula of species of *Fosterella*, such as the presence of weak adductor ridges, pointed basal ends of articular ridges, and strongly developed tergal depressor crests (the latter not present for *F. hennigi* (Newman, 1979) but that species has very distinctive elongate opercula). Furthermore, the shells of *Fosterella* are all strongly ribbed and, in addition to the defining character of multitubate parietes, have transverse septa in the parietal pores.

GEOLOGICAL SETTING

Austromegabalanus (Notomegabalanus) kensleyi is abundantly represented in a formation informally called the 50-metre Package (Pether 1986). This formation is comprised of gravels and fine sands laid down during regressive shoreline progradation from a transgressive maximum near 50 m above present sea-level. Depositional environments include the nearshore shelf (locally preserved only), lower shoreface, upper shoreface, foreshore, and back-barrier settings. The age of the 50-m Package is not yet unequivocally determined but is constrained by the presence of a remaniè vertebrate assemblage of Mio-Pliocene aspect at the base (Q. B. Hendey pers. comm.) and the occurrence of Equus near the top, the latter probably representing stratigraphic leakage from a closely overlying erosion surface. Furthermore, the highest elevation marine deposits (90-m Package, Fig. 1) inland of the 50-m Package have been correlated with the Early Pliocene Varswater Formation at Langebaanweg (Hendey 1981). The 50-m Package is thus considered to be Middle to Late Pliocene in age.

Austromegabalanus (Notomegabalanus) kensleyi has not been found in barnacle coquina from the 30-m Package, the regressive wedge overlying the transgressive truncation of the 50-m Package. Thus it appears to have become extinct on the Namaqualand coast around the Plio-Pleistocene. The lower limits of the new species are not yet determined, due to lack of material, but it is considered quite likely to extend into the Early Pliocene 90-m Package. At least one other species of barnacle is present in the 50-m Package. This is a non-megabalanine but opercula permitting determination have not yet been recovered.

In the barnacle coquina of the subsequent Early Pleistocene 30-m Package, disassociated opercula indicate the presence of three barnacle species, whereas parietal fragments indicate that *Austromegabalanus*, *Megabalanus* s.s. and *Balanus* species occur. The opercular material is too abraded for the purposes of unequivocal specific determination but one scutum type and one tergum type

(probably from the same species) appear sufficiently unique to suggest a new species. Other fragmentary opercula suggest that the *Austromegabalanus* sp. indicated by parietes may by *Austromegabalanus* s.s. It is hoped that continued fieldwork will produce better-preserved and associated examples of these taxa.

PALAEOENVIRONMENT

The types of A. (N.) kensleyi were found in situ on a boulder resting on the gneissic bedrock. The palaeoenvironment of the type area, reconstructed from the overlying sediments, was the inner, shallow portion of a protected embayment. The boulder was at shallow subtidal palaeodepth (<-5 m) when the live barnacles were covered by fine sands—probably during or immediately subsequent to a storm. Disarticulated barnacle fragments are a major component of coarse, basal lower shoreface deposits in the deeper portion of the bay and, within the fine sandy portion of the lower shoreface bay infill, the new species is commonly found encrusting Striostrea margaritacea (Lamarck) valves. These oysters were swept from the lower intertidal to shallow subtidal margin of the bay during storms and deposited in deeper water. Lagoonal deposits within which barnacle coquina lenses are present represent the final infilling of the embayment. These lenses are interpreted as coarser lags accumulated along the very shallow subtidal bases of tidal creeks within the lagoonal system, with barnacle fragments likely to have been transported by flood tides from the proximal lagoon and adjacent coast.

In exposed coastal settings, detached clusters of barnacles are found in shelly lenses within the storm-deposited lower shoreface facies. Disarticulated fragments are also an important component of the cross-stratified, coarse sandy upper shoreface facies.

In all the above instances the dominant barnacle is referable to the new species and its preferred environment was evidently the intertidal to shallow subtidal of normal marine salinity. The presence of warm-water West African and southern African east-coast molluscs in the 50-m Package indicates that the sea temperature was warmer than the present interglacial, at least seasonally. However, upwelling influences were present, as is attested by the occurrence of authigenic phosphorite rinds within nearshore shelf and basal lower shoreface facies. It is likely that changes in faunal structure associated with cooling, sea-level fall, and altered shelf currents account for the extinction of *A. (N.) kensleyi*.

CONCLUDING REMARKS

It is appropriate and not unexpected that the first extinct barnacle to be described from the coastal plain deposits of South Africa is a species of *Notomegabalanus*. Newman (1979) remarked that the austral region must have been richer in austral megabalanines during the Pliocene than it is today. The subsequent discovery of *Fosterella chathamensis* Buckeridge, 1983, from the

Pliocene of the Chatham Islands, *Austromegabalanus (A.) piscoensis* Carriol *et al.*, 1987, from the Pliocene of Peru, and the present species bears out that supposition that, with inclusion of the North American fossil species, may now be amplified to include both hemispheres during the Neogene.

Another species of *Austromegabalanus* is represented in the Early Pleistocene 30-m Package and may be *Austromegabalanus* s.s., but the abraded state of the available opercula preclude unequivocal specific identification at present. Significantly, material conclusively attributable to the extant South African *Austromegabalanus* species has not been recovered from the Upper Pliocene and Lower Pleistocene deposits. This suggests that *A. (A.) cylindricus* (Gmelin, 1780) does not have a range extending from the Pliocene, in contrast to *A. (A.) psittacus* (Molina, 1782) from South America. However, the former species is well represented in Last Interglacial beach deposits at Milnerton near Cape Town (Kensley 1985) and at other Late Pleistocene outcrops in the south-western Cape. *Austromegabalanus (N.) algicola* is also present in Last Interglacial deposits at Milnerton.

This paper represents the results of an initial reconnaissance of fossil barnacles from the Hondeklip study area. The recognition of a new species of barnacle from Pliocene coastal plain deposits, with possibilities of others in the future and as yet undetermined lower limits for extant South African Austromegabalanus species, holds the promise that barnacles will be of value in the correlation of the Late Tertiary and Quaternary shallow marine sequences of the southern African margin. Their calcitic composition favours preservation and, together with their abundance in shallow marine deposits, barnacle assemblages should emerge as useful biostratigraphic markers in the local coastal stratigraphy.

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